

A MUSCOIDES-LIKE *FUCUS* FROM A MAINE SALT MARSH: ITS ORIGIN, ECOLOGY, AND TAXONOMIC IMPLICATIONS

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ABSTRACT. The morphology and habitat of a dwarf moss-like or muscoides-like furoid brown alga were studied in the Brave Boat Harbor salt marsh of York-Kittery, Maine, U.S.A. using transect studies and transplant experiments. The plant, which lacks a holdfast, forms a dense embedded turf amongst sparse *Spartina patens* populations in the high marsh, particularly on well-drained sandy sediments near the Harbor's mouth. The plant's dichotomously branched fronds were smaller than those previously reported for muscoides-like populations from Europe (mean = 13.2 mm long, 1.1 mm wide, and 0.1 g damp-dried weight), while they had a similar dominance of marginal hair pits or cryptostomata. Transplantation of *in situ* *Fucus spiralis* from the lower to the upper marsh resulted in enhanced fragmentation, stunting, proliferation, and reduced reproduction. Reciprocal transplantation of the muscoides-like *Fucus* from upper to lower elevations caused enhanced frond length and proliferation. Based upon detailed transplant and morphological studies, we conclude that the muscoides-like *Fucus* plants from Brave Boat Harbor represent a phenotypic variant of *F. spiralis*, caused by detachment, extensive proliferation, and subsequent degeneration of detached fragments. The plant's dwarf morphology is primarily linked to a series of unique environmental conditions (desiccation and low nutrients), plus the type of attached parental material available. Thus, the dwarf muscoides-like *Fucus* in Europe and some Northwest Atlantic sites may be derived from *F. vesiculosus*, while in Brave Boat Harbor the parental material is *F. spiralis*. An analogous pattern is also evident between *Ascophyllum nodosum* and its detached ecad *scorpioides*, with the presence of dwarf specimens and the occurrence of a conspicuous morphological continuum between the two plants.

Key Words: Brave Boat Harbor Maine, ecad ecology, furoid algae, salt marsh algae, seaweed development, taxonomy

Seaweeds that lack holdfasts (free-living) are common throughout the world, particularly within protected embayments, salt marshes, and estuaries (Norton and Mathieson 1983). The temperate North Atlantic furoid genera *Ascophyllum* and *Fucus* contain several free-living salt marsh plants (Baker and Bohling 1916; Fritsch 1945; Niell et al. 1980), which can contribute major quantities of biomass and primary productivity (Brinkhuis 1976;

Brinkhuis and Jones 1976; Brinkhuis et al. 1976; Chock and Mathieson 1976). Several positive interactions occur between salt marsh flowering plants and unattached fucoids, including reduced desiccation and enhanced survival of *A. nodosum* (L.) Le Jolis ecad *scorpioides* (Hornemann) Reinke, plus increased cordgrass biomass (*Spartina alterniflora* Loisel.) due to enhanced sediment nutrients (Chapman and Chapman 1999; Gerard 1999). The taxonomy of unattached fucoids is poorly understood (Fritsch 1945; Norton and Mathieson 1983; Sears 1998), with plants being variously classified as ecads, megaecads, species, and varieties (Baker and Bohling 1916; Sears 1998; Taylor 1957; Wynne and Magne 1991). The “altered” morphology of free-living fucoids, which includes dwarfing, spiral twisting, profuse branching, vegetative propagation, and the lack of a holdfast (Baker and Bohling 1916; Fritsch 1945; Niell et al. 1980; Norton and Mathieson 1983) has contributed to these taxonomic problems. The varied morphologies of free-living fucoids have been attributed to reduced nutrients and/or salinities, sluggish currents, and enhanced desiccation (Boney 1966; Chapman 1964). In discussing the origin of free-living fucoids Fritsch (1945) emphasizes that they “are all derived by vegetative propagation from saxicolous types.”

One of the most unique marsh fucoids is the dwarf, embedded moss-like *Fucus* that is frequently found within upper salt marshes of Europe and the British Isles. It is described as being 5–6 cm tall, having cylindrical to compressed branches (1–3 mm wide), and bearing marginal hair pits or cryptostomata (cf. Fritsch 1945; Jorde 1966; Lynn 1935; Newton 1931; Valera and Cooke 1979). Although lacking a holdfast, the plant is anchored (i.e., partially embedded) in firm sand or peat-like sediments within high tidal marshes (Cotton 1912; Feldmann and Magne 1964; Lynn 1935; Norton and Mathieson 1983). Muscooides-like *Fucus* plants have been variously designated as varieties (Cotton 1912; Lynn 1935), ecads (Baker and Bohling 1916; Niell et al. 1980), or as distinct species (Feldmann and Magne 1964; Parke and Dixon 1976; Wynne and Magne 1991). In Cotton’s (1912) initial characterization of this muscooides-like *Fucus*, he treated it taxonomically as *F. vesiculosus* L. var. *muscooides* and described it as forming moss-like carpets (i.e., swards) within the high intertidal zone at Clare Island, Ireland. Subsequently Baker and Bohling (1916) designated the plant as *F. vesiculosus* ecad *muscooides*,

emphasizing that it was part of a morphological cline within the megaecad *limicola* Baker *et* Bohling (Clements 1905); the ecads *caespitosus* Baker *et* Bohling, *filiformis* J. Agardh, *nanus* J. Agardh, *subecostatus* J. Agardh, and *volubilis* (Hudson) Turner were also included within the megaecad *limicola* of *F. vesiculosus*. Feldmann and Magne (1964) elevated *F. vesiculosus* var. *muscoides* to a distinct species, *F. muscoides*. On the other hand, during a recent survey of Spanish *F. vesiculosus* populations, Niell *et al.* (1980) agreed with Baker and Bohling's (1916) interpretation, designating various ecads within *F. vesiculosus* megaecad *limicola* and showing a gradation of morphology ranging from *F. vesiculosus* f. *axillaris* to *F. vesiculosus* ecads *volubilis*, *caespitosus*, and *muscoides*.

Wynne and Magne (1991) also agreed with Feldmann and Magne (1964), stating that this plant should be recognized at the species level. However, they pointed out that the name employed by Feldmann *et* Magne (1964), namely *Fucus muscoides* (Cotton) Feldman and Magne, created a later homonym of a red alga now known as *Acanthophora muscoides* (L.) Bory de Saint-Vincent (1828). Accordingly they proposed a new name, *F. cottonii* M. J. Wynne *et* Magne, in honor of A. D. Cotton, suggesting that the dwarf morphology and unique ecological niche within high tidal marshes clearly delineated the taxon.

The present study was undertaken after a floristic investigation of seaweeds within Brave Boat Harbor, York-Kittery, Maine, U.S.A. (Figure 1) revealed the first occurrence of a muscoides-like *Fucus* plant in North America (Mathieson *et al.* 2001). In the present account we summarize detailed morphological, ecological, and transplant data regarding these unique populations, in order to clarify the plant's origin, taxonomy, and biology.

MATERIALS AND METHODS

Mathieson *et al.* (2001) have given a detailed characterization of the Brave Boat Harbor salt marsh (43°06.0'N, 70°39.33'W; hereafter BBH), including its geography, hydrographic conditions (temperature and salinity), habitat variability, species composition, and site locations within the main tidal channel and four contiguous tidal tributaries. The biomass patterns for the muscoides-like *Fucus* and other salt marsh plants were recorded at seven transect sites along the main tidal channel (Figure 1), with

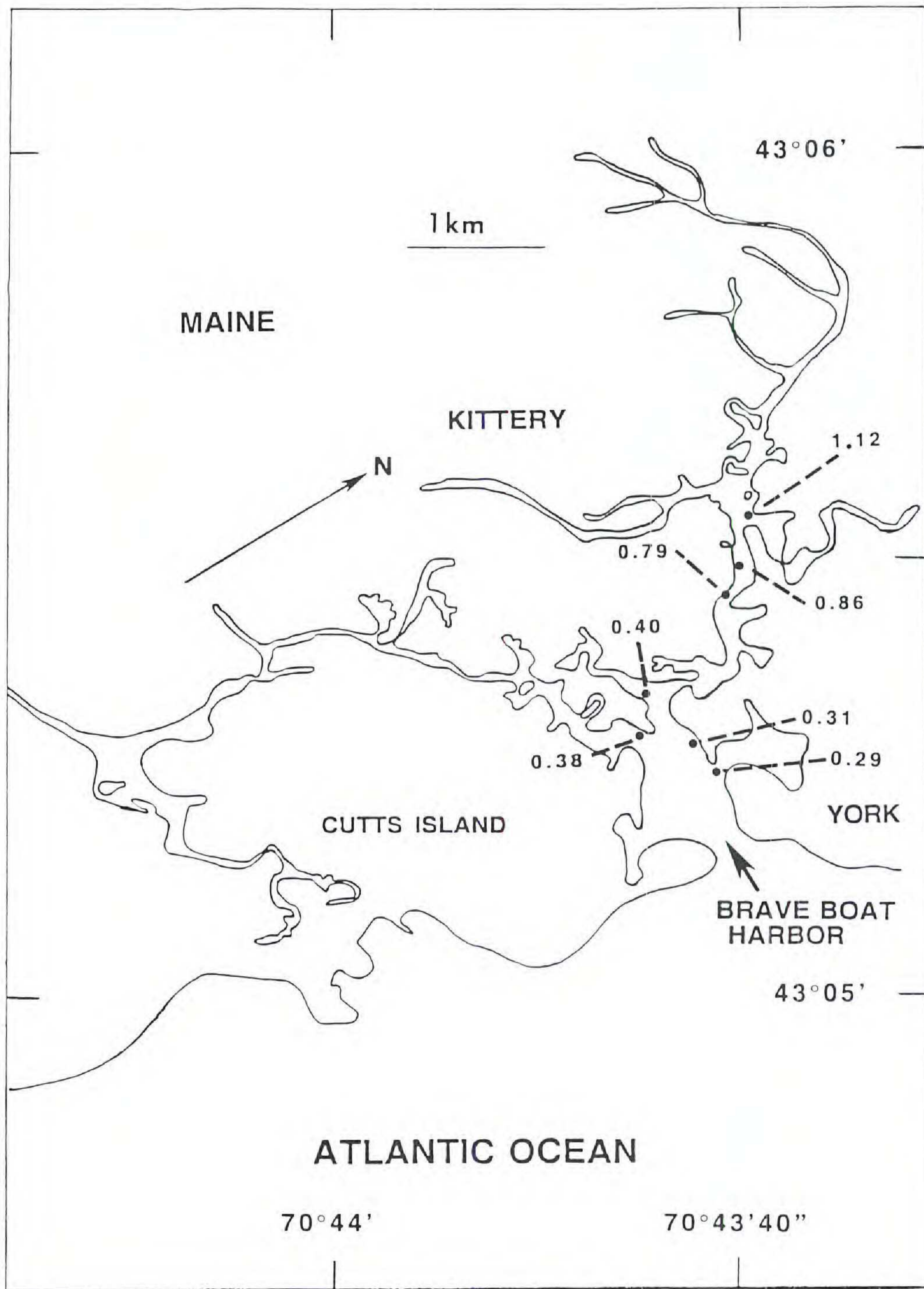


Figure 1. Brave Boat Harbor, York-Kittery, Maine showing the location of seven transect sites within the main tidal channel. See Figure 1 in Mathieson et al. (2001) for details of the southern Maine coast.

Table 1. Distribution and mean biomass of dominant seaweeds and flowering plants on seven transects within Brave Boat Harbor, Maine. Symbols: % = percent occurrence, × = present, and mean biomass = g dry wt./m² ± 1 SD (± 1 SE).

Site #	1	2	3	4	5	6	7		Mean Biomass
Distance inland from mouth (km)	0.29	0.31	0.38	0.40	0.79	0.86	1.12	%	(sites present)
SEAWEEDES									
<i>Ascophyllum nodosum</i> (L.) Le Jolis	×						×	28.6	20.5 ± 14.8 (10.6)
<i>Ascophyllum nodosum</i> (L.) Le Jolis ecad <i>scorpioides</i> (Hornemann) Reinke		×	×	×	×	×	×	85.7	868.2 ± 1255.0 (500)
<i>Fucus</i> sp. "muscooides-like"	×	×	×	×	×	×	×	100	266.3 ± 122.3 (46.2)
<i>Fucus spiralis</i> L.	×	×	×	×	×	×		85.7	327.8 ± 395.0 (161.4)
<i>Fucus spiralis</i> L. ecad <i>lutarius</i> (Kützting) Sauvageau		×						14.3	130.0 ± 94.8 (94.8)
<i>Fucus vesiculosus</i> L. ecad <i>volubilis</i> (Hudson) Turner						×	×	28.6	647.8 ± 590.8 (341.5)
<i>Melanosiphon intestinalis</i> (D. A. Saunders) M. J. Wynne	×	×	×	×	×	×	×	57.1	378.6 ± 124.0 (62.0)
<i>Rhizoclonium riparium</i> (Roth) Harvey	×	×	×	×	×	×	×	100	112.6 ± 108.8 (41.1)
<i>Vaucheria</i> spp.									
TOTAL SEAWEEDES/SITE	6	7	6	6	6	5	6		

Table 1. Continued.

Site #	1	2	3	4	5	6	7		Mean Biomass
Distance inland from mouth (km)	0.29	0.31	0.38	0.40	0.79	0.86	1.12	%	(sites present)
[Mean # taxa = 6.0 ± 0.57; Mean % = 66.9 ± 35.1%; Mean Biomass (sites present) = 313.8 ± 281.0 (93.7) g dry wt./m ²]									
FLOWERING PLANTS									
<i>Festuca rubra</i> L.					×	×		28.6	5095.7 ± 4159.2 (2949.8)
<i>Limonium nashii</i> Small	×	×	×	×	×	×		85.7	226.0 ± 229.6 (93.7)
<i>Salicornia europaea</i> L.			×					14.3	28.0 ± 38.9 (38.9)
<i>Spartina alterniflora</i> Loisel.		×	×	×	×	×	×	85.7	298.6 ± 367.0 (149.8)
<i>Spartina patens</i> (Aiton) Muhl.	×	×	×	×	×	×	×	100	915.9 ± 968.9 (365.6)
<i>Suaeda maritima</i> (L.) Dumort.					×			14.3	253.0 ± 238.3 (238.3)
<i>Triglochin maritima</i> L.						×		14.3	63.0 ± 89.1 (89.1)
TOTAL FLOWERING PLANTS/SITE	2	3	4	3	5	5	2		
[Mean # taxa = 3.4 ± 1.3; Mean % = 49.0 ± 39.4%; Mean Biomass (sites present) = 982.8 ± 1836.9 (693.2) g dry wt./m ²]									

these sites varying from 0.29 km to 1.12 km inland from the mouth. Elevation records were determined using a line level and a surveying rod (Dawes 1998; Mathieson et al. 1998), with vertical heights above or below mean low water (i.e., MLW) being calculated from predicted tidal levels (Harbor Master Program, Version 3, Zihua Software, Marlboro, CT). The delay in tidal rise for inner transect sites was calculated by subdividing the main channel into four 15-minute increments that matched the one-hour delay noted at the innermost part of the marsh.

Transect studies (Figure 1) were conducted between May and September, 1998 at seven sites. Metered lines of variable lengths (5–7 m), depending upon shore topographies, were established at right angles to the shoreline, extending from the tidal channel to the high marsh community dominated by *Spartina patens* (Aiton) Muhl. A minimum of two biomass cores per meter were taken along each transect with a polyvinylchloride tube (95 cm²), particularly when conspicuous vegetational changes occurred or where the muscoides-like *Fucus* was evident. Each core was labeled and returned to the laboratory within one hour where it was stored at 10°C until being processed. Ultimately the macroalgae and salt marsh plants within each core were separated and their damp-dried biomass values converted to g dry wt./m² using a wet to dry weight conversion determined for each species. A comparison of species composition and mean biomass for the seven transects is summarized (Table 1). Morphological assessments of five of the six furoid taxa found were made, including *Fucus spiralis* L., *Ascophyllum nodosum* (L.) Le Jolis ead *scorpioides* (Hornemann) Reinke, *F. spiralis* ead *lutarius* (Kützing) Sauvageau, *F. vesiculosus* L. ead *volubilis* (Hudson) Turner, and the muscoides-like *Fucus* (Figures 2 and 3).

Reciprocal transplants of cores (92 cm²) containing *Fucus spiralis* and muscoides-like *Fucus* plants were initiated during June 1998 at a site located 0.38 km inland from the mouth along the main tidal channel of BBH. Vertical transfers were made from +2.0 to +3.4 m above MLW and vice versa, with four different types of populations being assessed: (1) high *in situ* populations of muscoides-like *Fucus* or a mixture of fragmented *F. spiralis* ead *lutarius* and muscoides-like plants; (2) low *in situ* *F. spiralis*; (3) low transplants or plants that were transferred from the higher to the lower furoid zone; and (4) high transplants or plants that were transferred from the lower to the higher furoid zone.

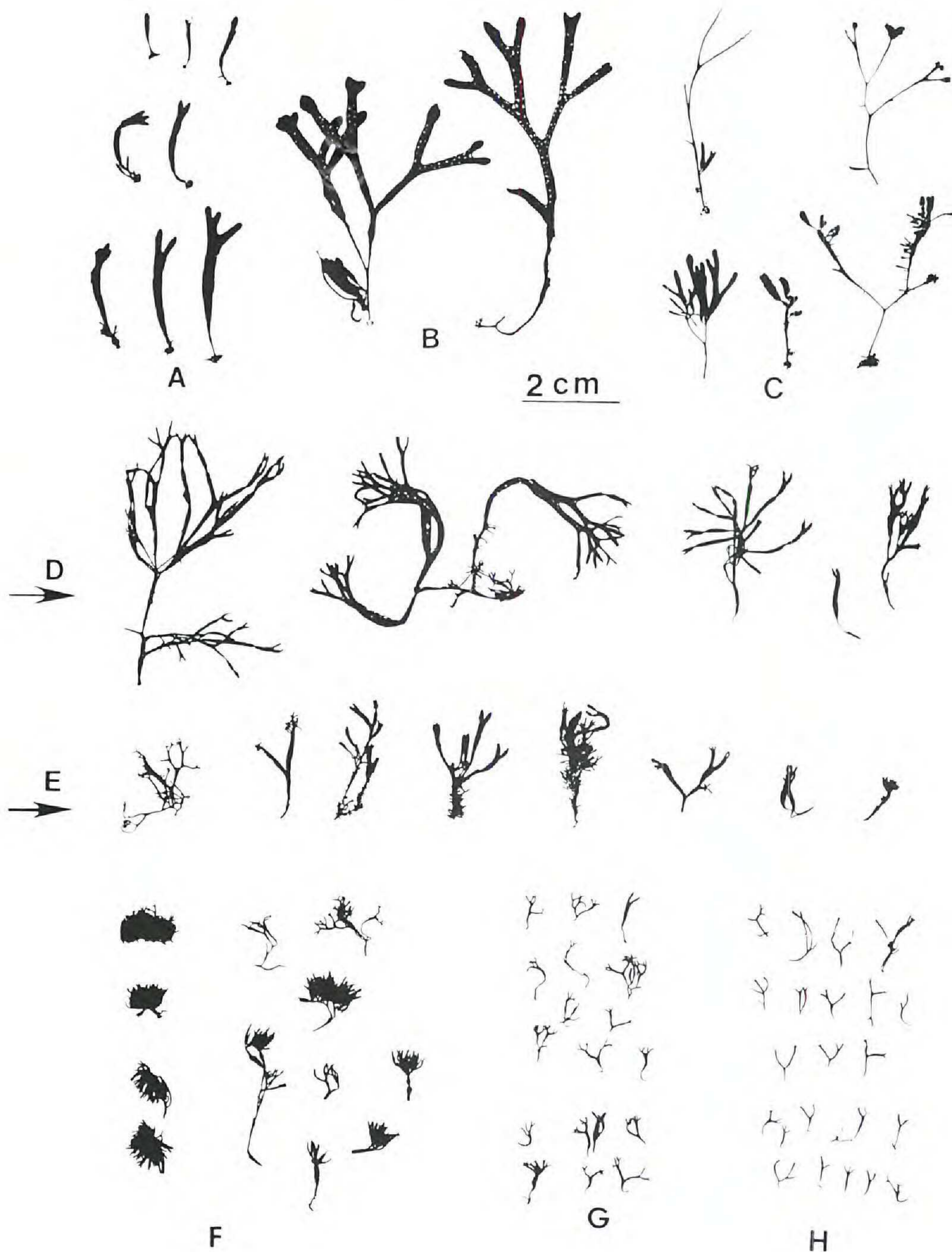


Figure 2. Silhouettes of morphological variability in three fucoid populations from Brave Boat Harbor. Attached *Fucus spiralis* ranging from germlings (A, group of 8), to a pair of reproductively mature adults (B), to residual and proliferous specimens (C, group of 5). Detached specimens of *F. spiralis* ecad *lutarius* grading from large, fragmented fronds (D, group of 5), to more proliferous, smaller plants (E, group of 8). Turf-like populations of muscooides-like *Fucus* ranging from tufted, elongated specimens (F, group of 12), to short, individual fronds (G, group of 18), to minute plants (H, group of 22).



Figure 3. Silhouettes of morphological variability in two fucoid taxa from Brave Boat Harbor, Maine. Detached *Ascophyllum nodosum* grading from two large fragments (A), to a pair of more proliferous fragments (B), to progressively smaller fronds (C, group of 6), and finally to minute plants of the ecad *scorpioides* (D, group of 11). Attached (E) and detached fronds of *Fucus vesiculosus* (F) grading into *F. vesiculosus* ecad *volubilis* (G, group of 3), and then to more proliferous and smaller residual specimens (H, group of 3).

Table 2. Sediment characteristics of core samples (top 5 cm) from each of seven transect sites within Brave Boat Harbor's main tidal channel. The data represent percentages \pm 1 SD of total values based on the means of duplicate cores.

Site #	Mean % total composition \pm 1 SD						
	1	2	3	4	5	6	7
Distance inland (km)	0.29	0.31	0.38	0.40	0.79	0.86	1.12
Water content (%)	26.0 \pm 0.9	30.0 \pm 2.4	37.0 \pm 1.2	36.0 \pm 1.5	51.0 \pm 2.3	54.0 \pm 0.5	55.0 \pm 0.7
Medium size particles ($>$ 0.125 mm)	70.0 \pm 8.1	55.0 \pm 6.6	58.0 \pm 8.8	58.0 \pm 14.0	30.0 \pm 7.4	32.0 \pm 7.4	33.0 \pm 3.1
Fine sand, silt parti- cles ($<$ 0.063 mm)	3.0 \pm 1.0	3.0 \pm 1.3	4.0 \pm 1.3	5.0 \pm 1.3	10.0 \pm 1.7	11.0 \pm 2.5	11.0 \pm 3.4

Thus, the terms low and high transplants refer to the resulting rather than the initial materials. Duplicate cores of each *in situ* population were taken in order to evaluate initial biomass and morphometric patterns (see below). The transplant samples were harvested after approximately one year (i.e., June 1999) and several morphometric features were compared with previous *in situ* materials (see above).

Replicate core samples at individual transect sites were pooled and the frond morphology of 25 plants assessed, including their length (cm), width (mm), weight (g), burial depth (mm) or the blackened zone due to anoxic conditions, numbers of branches and fertile tips, and numbers of marginal and surficial cryptostomata or hair pits (cf. Niell et al. 1980). Only flattened fronds of *Fucus* plants were assessed for cryptostomatal patterns, as the small cylindrical branches of the muscooides-like *Fucus* had few cryptostomata and could not be directly compared with other flattened taxa. Cryptostomatal ratios were assessed using a representative ocular field (100 \times). Ultimately, mean values and standard deviations for each of the above described morphometric parameters were calculated.

Sediment particle size and water content were determined at each of the seven transect sites (Table 2), using a stainless steel tube (11.3 cm²). Duplicate cores (10 cm long) were extracted at each site within dense populations of muscooides-like *Fucus* and placed in individually labeled plastic bags that were returned to the laboratory. Samples were either processed immediately or refrigerated at 10°C for later analysis. The above-ground plant ma-

terial was removed, including the attached and/or buried seaweed samples, and the cores were oven dried at 60°C for 48 hours. Percent water of each core was determined by weighing samples before and after drying, with the measurements having an accuracy of ± 0.01 g. Dried samples were sieved for particle size.

RESULTS

Ecology of muscoides-like *Fucus*. As shown in Table 2, surface sediments within BBH are sandy, with those in the outer to middle channel (0.29–0.40 km) having 55 to 70% medium-sized sand particles (> 0.125 mm diameter). By contrast, inner sites (0.79–1.12 km) show a decrease in coarse particles and an enhancement of very fine sand, clay, and silt (< 0.063 mm). The percentage of pore water showed a conspicuous increase from 0.29–1.12 km inland (Table 2). Hence, there was more extensive standing water and enhanced filamentous algae (i.e., one or more species of *Vaucheria* and *Rhizoclonium riparium*) at inner than outer sites (see below).

Nine seaweed taxa and seven flowering plant species were found on the seven transects (Table 1). The muscoides-like *Fucus*, *Rhizoclonium riparium*, and *Vaucheria* spp. were the most cosmopolitan seaweeds (100% occurrence), followed by *Ascophyllum nodosum* ead *scorpioides* (85.7%), *F. spiralis* (85.7%), *Melanosiphon intestinalis* (D. A. Saunders) M. J. Wynne (57.1%), *A. nodosum* (28.6%), *F. vesiculosus* ead *volubilis* (28.6%), and *F. spiralis* ead *lutarius* (14.3%). The most ubiquitous flowering plants were *Spartina patens* (100% occurrence), *Limonium nashii* Small (85.7%), and *S. alterniflora* (85.7%), with rare occurrences of *Salicornia europaea* L., *Suaeda maritima* (L.) Dumort. and *Triglochin maritima* L. (14.3%). Overall, the mean number of taxa and the percentage occurrence of seaweeds on the various transects were 6.0 ± 0.57 taxa and $66.9 \pm 35.1\%$, respectively, versus 3.4 ± 1.3 taxa and $49.0 \pm 39.4\%$ for flowering plants (Table 1). Of the six furoid algae, two grew attached (*Ascophyllum nodosum* and *Fucus spiralis*), three occurred as entangled/buried plants (*A. nodosum* ead *scorpioides*, *F. spiralis* ead *lutarius*, and *F. vesiculosus* ead *volubilis*), and one (the muscoides-like *Fucus*) formed embedded, turf-like masses. The filamentous green alga *Rhizoclonium riparium* produced extensive, entangled masses on muddy surfaces (see below), while the sediment-in-

habiting yellow-green algal genus *Vaucheria* often grew with it. The tubular brown alga *Melanosiphon intestinalis* grew on erosive, sandy cliffs at outer-middle sites. No attached populations of *F. vesiculosus* were found on any of the transects (see below).

Table 3 illustrates biomass patterns on two transect sites located at 0.40 km and 0.79 km inland. The outer transect was ~4.6 m long and had a gradual slope (~0.26 m vertical/1.0 m horizontal), while the inner one was shorter (~3.5 m) and had a steeper shoreline (~0.34 m vertical/1.0 m horizontal). In comparing biological patterns, the muscoides-like *Fucus* at the 0.40 km transect had a greater biomass, it extended higher vertically (+3.0 to +3.4 m), and was primarily associated with *Spartina patens*. By contrast, plants growing at the inner site exhibited a reduced biomass, a more circumscribed zonation (i.e., +1.8 to +2.4 m), and were usually associated with *S. alterniflora*. Although not illustrated, the plants' horizontal distribution (i.e., belt) on the seven transects also varied spatially, being 2.1 ± 1.8 m (0.90) between 0.29–4.0 km, 0.92 ± 0.174 m (0.3) at 0.79–1.12 km, and averaging overall 1.6 ± 1.5 m (1.2) for the seven sites. Thus, inner populations typically formed narrow belts adjacent to vertical bluffs, while they were more expansive towards the mouth.

As shown in Table 3, *Fucus spiralis* and *Melanosiphon intestinalis* were the most abundant seaweeds on the outer transect and were either reduced or absent at the inner site. *Ascophyllum nodosum* ecad *scorpioides*, *Spartina alterniflora*, and *S. patens* all showed the opposite pattern, being more abundant at inner than outer sites. *Spartina patens* also occurred at lower elevations at 0.40 km (~+1.6 to +2.4 m) than 0.79 km inland (~+3.1 m). *Fucus vesiculosus* ecad *volubilis* was only found within the low intertidal at 0.79 km. *Fucus spiralis* and the muscoides-like *Fucus* populations exhibited contrasting vertical distributions at the outer site, with the former dominating the lower and the latter the upper shoreline.

Figure 4 illustrates spatial biomass patterns for six fucoid taxa, with the data being expressed as mean biomass values (i.e., g dry wt./m²) per transect. Populations of the muscoides-like *Fucus* (Figure 4A) were maximal (286.0 ± 24.7 to 389.0 ± 420.0 g dry wt./m²) at the three outer sandy sites (i.e., 0.29–0.38 km, Table 1), while they varied from 28.0 ± 8.5 to 208.0 ± 141.4 g dry wt./m² at the inner more silty sites (i.e., 0.79–1.12 km, Table 1). *Fucus spiralis* exhibited its maximum and minimum biomass

Table 3. Biomass patterns versus height above mean low water (MLW) for dominant intertidal plants at two transect sites within Brave Boat Harbor's main tidal channel. Symbols: ANS = *Ascophyllum nodosum* ecad *scorpioides*, FMUSC = muscoides-like *Fucus*, FS = *F. spiralis*, FVV = *F. vesiculosus* ecad *volubilis*, MI = *Melanosiphon intestinalis*, SA = *Spartina alterniflora*, and SP = *S. patens*.

Height above MLW (m)	Biomass (g dry wt./m ² ± 1 SD)						
	ANS	FMUSC	FS	FVV	MI	SA	SP
INNER TRANSECT (0.40 km)							
+2.2	0	0	627.0 ± 23.0	0	278.0 ± 7.0	12.0 ± 6.0	0
+2.4	0	0	145.0 ± 33.0	0	379.0 ± 130.0	16.0 ± 2.0	0
+2.8	0	0	144.0 ± 105.0	0	314.0 ± 136.0	0	0
+3.0	65.0 ± 39.0	82.0 ± 44.0	289.0 ± 7.0	0	0	0	691.0 ± 680.0
+3.2	12.0 ± 2.0	170.0 ± 21.0	44.0 ± 31.0	0	0	27.0 ± 27.0	367.0 ± 114.0
+3.4	4.0 ± 4.0	258.0 ± 111.0	16.0 ± 16.0	0	0	241.0 ± 100.0	1387.0 ± 522.0
OUTER TRANSECT (0.79 km)							
+1.6	2998.0 ± 173.0	0	0	1941.0 ± 768.0	0	1333.0 ± 242.0	0
+1.8	168.0 ± 87.0	34.0 ± 15.0	18.0 ± 18.0	0	0	0	0
+2.2	7688.0 ± 421.0	0	0	190.0 ± 112.0	0	777.0 ± 100.0	0
+2.4	37.0 ± 5.0	22.0 ± 11.0	0	0	0	405.0 ± 179.0	1985.0 ± 559.0
+2.6	0	0	0	0	0	111.0 ± 14.0	4126.0 ± 713.0
+2.8	0	0	0	0	0	0	0

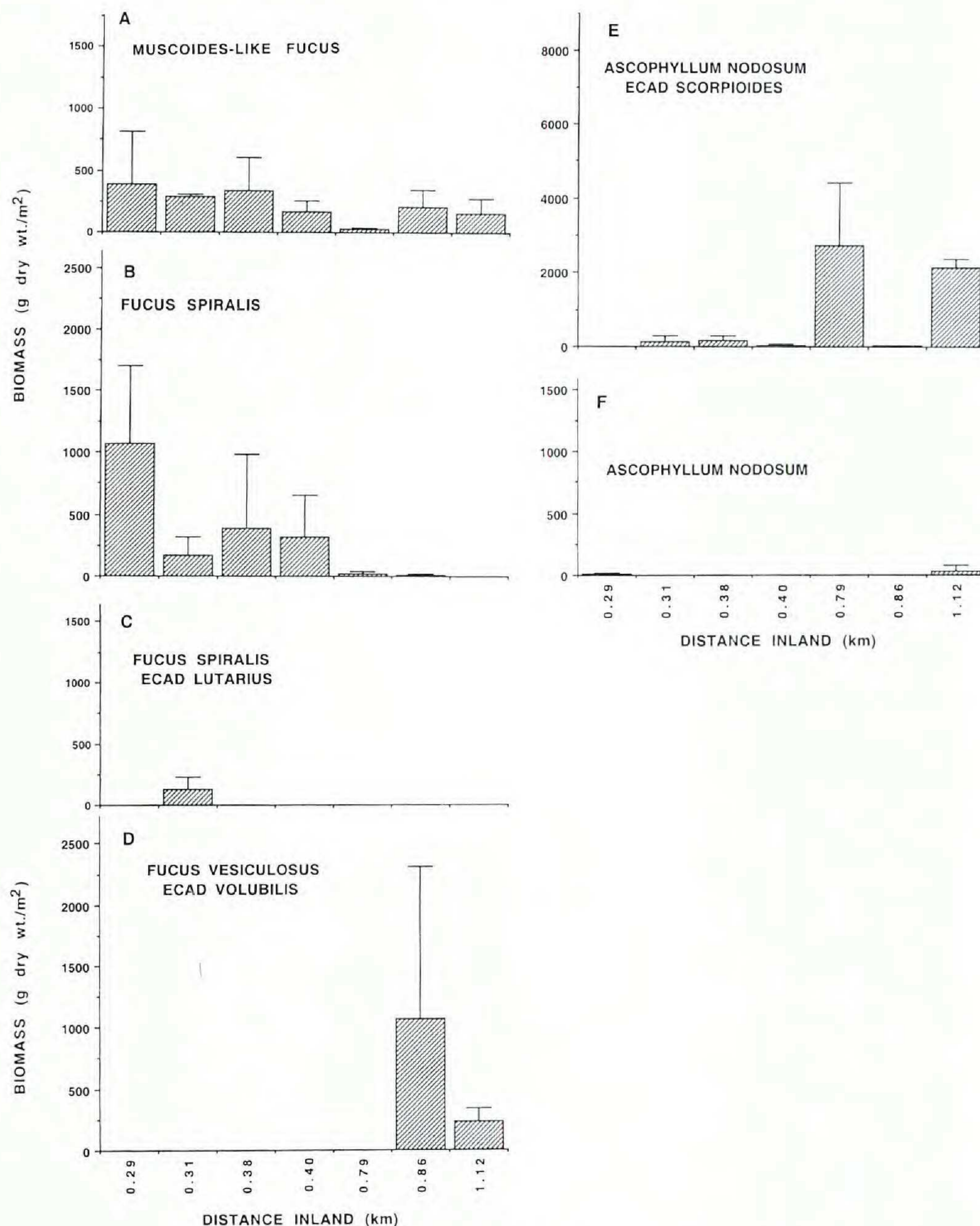


Figure 4. Mean biomass patterns (g dry wt./m² ± 1 SD) for muscooides-like *Fucus* (A), *F. spiralis* (B), *F. spiralis* ecad *lutarius* (C), *F. vesiculosus* ecad *volubilis* (D), *Ascophyllum nodosum* ecad *scorpioides* (E), and *A. nodosum* populations (F) on seven transects within Brave Boat Harbor's main tidal channel, with the sites ranging from 0.29–1.12 km inland.

(Figure 4B) at 0.29 km (1072.5 ± 632.9 g dry wt./m²) and 0.86 km (8.5 ± 12.0 g dry wt./m²), respectively. The three entangled fucoid ecads *F. spiralis* ecad *lutarius*, *F. vesiculosus* ecad *volubilis* and *Ascophyllum nodosum* ecad *scorpioides* exhibited contrasting distributional patterns (Figures 4C–E). *Fucus spiralis*

ecad lutarius was only found at the 0.31 km site (130.0 ± 94.8 g dry wt./m²), while *F. vesiculosus ecad volubilis* was present at 0.86 km (1065.6 ± 1238.1 g dry wt./m²) and 1.12 km inland (230.0 ± 111.7 g dry wt./m²). The mean biomass for *A. nodosum ecad scorpioides* varied from 0 to 2722.0 ± 1704.5 g dry wt./m² (Figure 4E), with the highest values occurring at inner silty sites (i.e., 0.79 and 1.12 km). Attached populations of *A. nodosum* were uncommon (10.0 ± 13.4 to 31.0 ± 43.8 g dry wt./m²) and only occurred at the outer- and innermost sites.

The overall mean biomass patterns for various seaweeds and flowering plants on the seven transects are summarized in Table 1. Of the six furoid algae, *Ascophyllum nodosum ecad scorpioides* was the dominant taxon, followed by *Fucus vesiculosus ecad volubilis*, *F. spiralis*, the muscoides-like *Fucus*, *F. spiralis ecad lutarius*, and *A. nodosum*. Overall, *A. nodosum ecad scorpioides* was the dominant species (868.2 ± 1225.0 g dry wt./m²), while *A. nodosum* was the least abundant (20.5 ± 14.8 g dry wt./m²); the muscoides-like *Fucus* exhibited an intermediate pattern (226.3 ± 122.3 g dry wt./m²) relative to the other taxa. Regarding the flowering plants, the mean biomass was 982.8 ± 1836.9 g dry wt./m² with this varying from 28.0 ± 38.9 (*Salicornia europaea*) to 5095.7 ± 4159.2 g dry wt./m² (*Festuca rubra*). Thus, the mean number and percent occurrence of seaweed taxa per site were higher than for flowering plants, while the biomass values for flowering plants exceeded that of the seaweeds.

As shown in Table 1, the muscoides-like *Fucus* exhibited varying affinities with the other five furoid taxa. Thus, it occurred at 6 of the 7 sites where *F. spiralis* and *Ascophyllum nodosum ecad scorpioides* were found (85.7% similarity), while it exhibited a reduced affinity with *A. nodosum* (28.6%), *F. vesiculosus ecad volubilis* (28.6%), and *F. spiralis ecad lutarius* (14.3%). The muscoides-like *Fucus* was also consistently found in association with the sediment-inhabiting *Vaucheria* spp.–*Rhizoclonium riparium* complex, plus the flowering plant *Spartina patens* (100% similarity). *Limonium nashii* and *S. alterniflora* also showed a strong affinity to the muscoides-like *Fucus*, with populations occurring together at six of the seven sites (i.e., 85.7% similarity). Based on the above information the following comments can be made: (1) the muscoides-like *Fucus*, *F. spiralis*, and *A. nodosum ecad scorpioides* exhibited very similar distributional patterns, albeit the muscoides-like plants and *A. nodosum ecad scorpioides* had

contrasting ecological requirements (cf. Table 2; Figure 4A, E); (2) attached *in situ* *A. nodosum* and *F. spiralis* and their corresponding detached ecads (i.e., *A. nodosum* ecad *scorpioides* and *F. spiralis* ecad *lutarius*) also had different ecological requirements (cf. Figure 4B, C, E, F); (3) *F. vesiculosus* was only represented on the transects by its ecad *volubilis*, with a few attached and scattered populations occurring within the main tidal channel and adjacent open coast (Mathieson et al. 2001); and (4) the muscoides-like *Fucus* was typically found beneath the canopy of sparse *Spartina patens*, often growing in association with the *Vaucheria* spp.–*Rhizoclonium riparium* complex.

Furoid morphology. Figure 5 presents six morphological features for the muscoides-like populations at seven sites within BBH, expressed as mean values \pm SD per site. Few obvious patterns were evident, except for a diminishment of burial depths from the outermost site inland (Figure 5D) and a dominance of marginal versus surficial pits (Figure 5F). Overall, frond length (Figure 5A) varied from 11.2–16.1 mm (mean = 13.2 ± 4.2 mm), width (Figure 5B) from 0.9–1.4 mm (mean = 1.1 ± 0.2 mm), weight (Figure 5C) from 0.1–0.17 g (mean = 0.1 ± 0.03 g), burial depth (Figure 5D) from 3.1–8.3 (mean = 5.6 ± 1.8 mm), number of branches per frond (Figure 5E) from 3.4–6.9 (mean = 4.6 ± 1.1), and numbers of marginal and surface pits (Figure 5F) from 1.0–15.8 (mean = 8.1) and 0.0–1.65 (mean = 0.74), respectively. Overall, the mean ratio of marginal to surface pits was 11:1.

Figure 6 summarizes horizontal and vertical differences in stature and morphology for two populations of the muscoides-like *Fucus* (0.29 and 0.40 km), expressed as mean values \pm SD. Typically plants from lower elevations were longer than those from upper ones (Figure 6A), with the smallest plants (14.4 ± 4.3 mm) occurring at the outer, upper site and the largest at the lower, inner location (28.9 ± 12.1 mm). Frond width and weight (Figure 6B, C) were widest and heaviest at lower elevations. Burial depth (Figure 6D) was more circumscribed at outer (6.6–6.8 mm) than inner (8.7–12.9 mm) sites. The high numbers of branches per frond (Figure 6E) at the lower, inner site (17.9 ± 26.1) are indicative of extensive proliferations (cf. Figure 2F), with the other three samples having limited proliferations and lower numbers of branches per frond (i.e., 7.2–12.5). Fronds of the muscoides-like

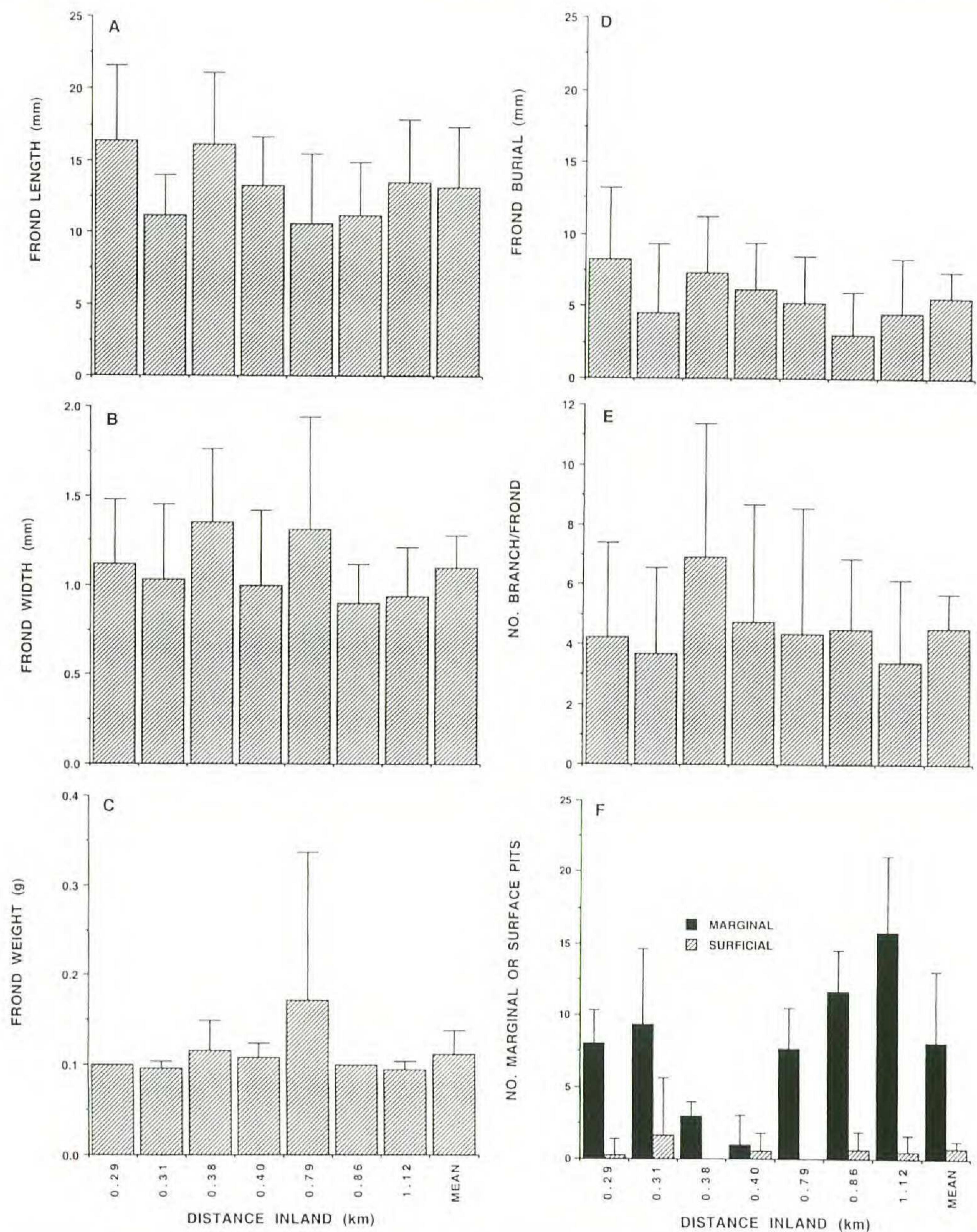


Figure 5. A synopsis of six morphological features (± 1 SD) for muscoides-like *Fucus* populations at seven locations within Brave Boat Harbor's main tidal channel (0.29–1.12 km inland), expressed as mean site values (\pm SD) for frond length (A), frond width (B), frond weight (C), burial depth (D), number of branches per frond (E), and number of marginal and surficial pits (F); the overall mean values for each parameter are also shown.

Fucus were dominated by marginal pits (Figure 6F), with the occurrence of surficial pits being inconsistent and reduced in numbers.

Figure 7 demonstrates morphological features for seven *Fucus spiralis* populations within BBH, expressed as mean values \pm SD

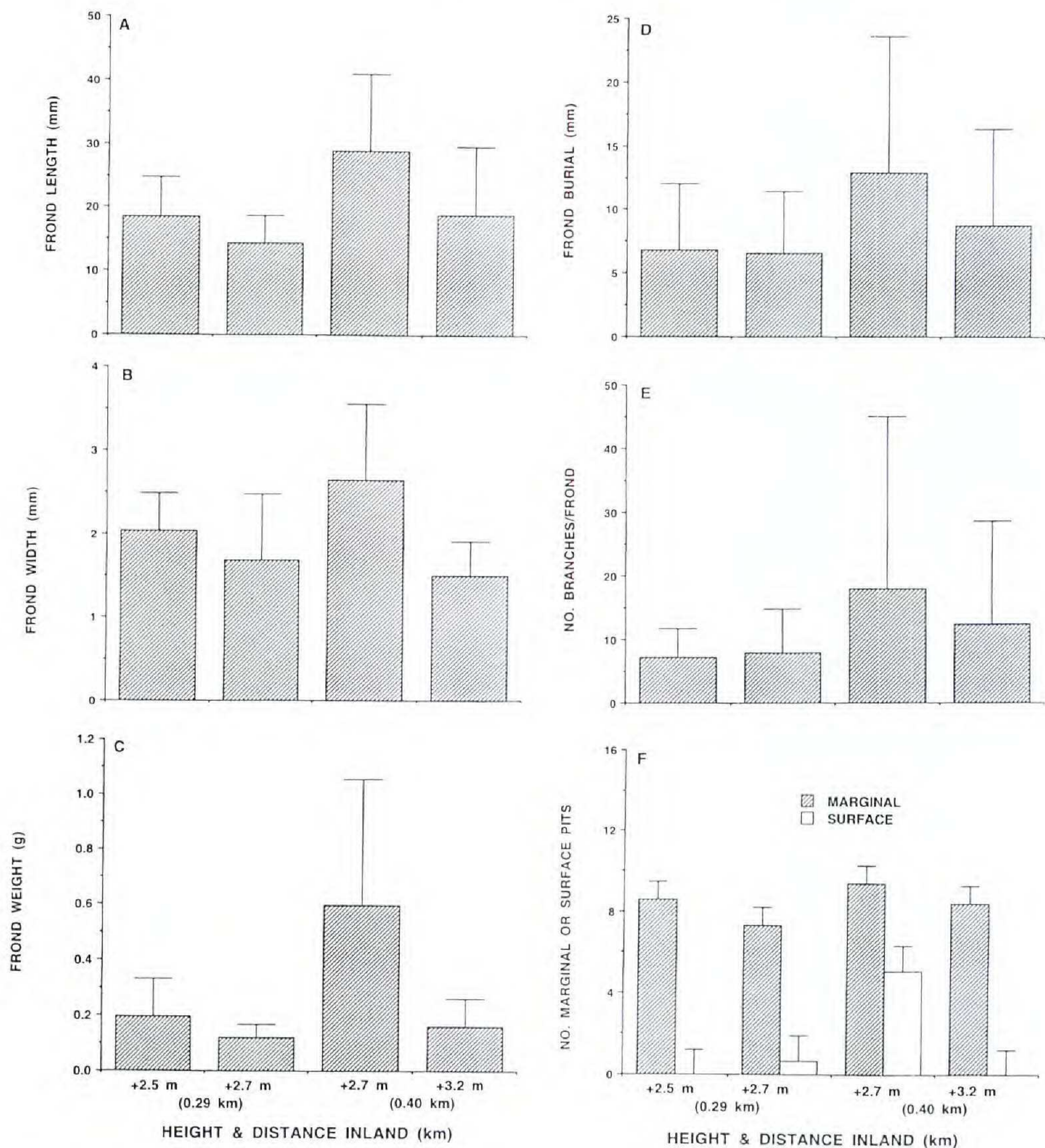


Figure 6. A synopsis of six morphological features (± 1 SD) for Brave Boat Harbor muscooides-like *Fucus* at two sites (0.29 and 0.40 km inland) and multiple elevations (+2.5 and +2.7 m versus +2.7 and +3.2 m), with the values being expressed as mean frond length (A), width (B), weight (C), burial depth (D), number of branches per frond (E), and number of marginal and surficial pits (F).

per site. The smallest, narrowest, and lightest fronds occurred at the innermost estuarine site (0.79 km) where the species occurred (18.5 ± 3.5 mm, 3.3 ± 0.4 mm, and 0.6 ± 0.01 g, respectively; Figure 7A–C). Analogous patterns occurred for the numbers of branches per frond and reproductive tips (Figure 7D, E). By contrast, these same parameters were relatively uniform (e.g., length and width), decreased clinally (weight), or were quite variable at outer-middle sites (e.g., # of branches and fertile tips). Fronds of

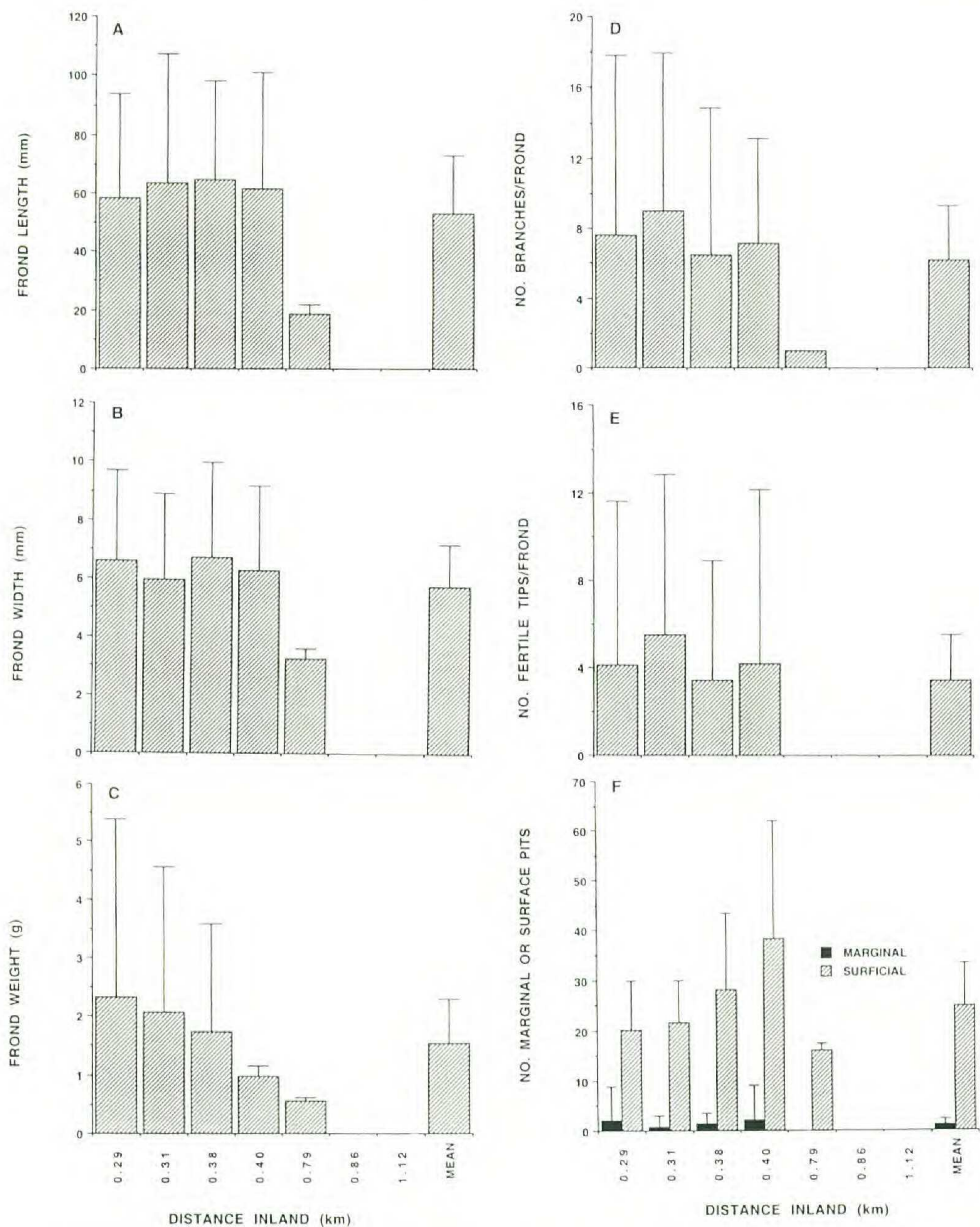


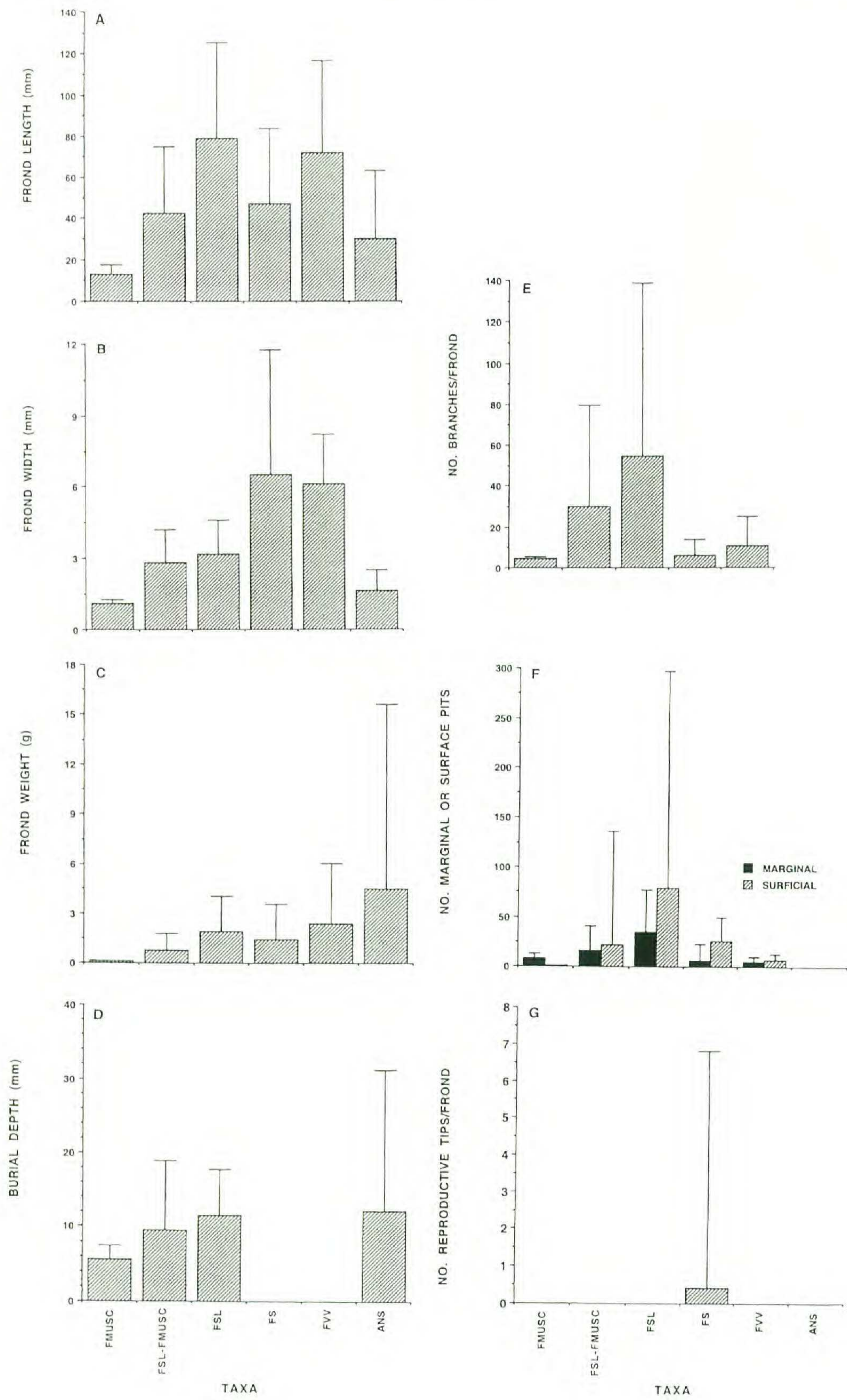
Figure 7. A synopsis of six morphological features (± 1 SD) for *Fucus spiralis* populations at seven locations within Brave Boat Harbor's main tidal channel (0.29–0.86 km inland), expressed as mean site values (\pm SD) for frond length (A), width (B), weight (C), number of branches per frond (D); number of fertile tips per frond (E); and number of marginal and surficial pits (F); the overall means (\pm SD) for each parameter are also shown.

F. spiralis had fewer marginal (0.0–2.2, mean = 1.3 ± 0.9) than surficial pits (16.0–38.2, mean = 24.8 ± 8.6), which contrasts with the situation in the muscoides-like *Fucus* (cf. Figures 5F, 7F). The overall mean values for *F. spiralis* fronds were $53.4 \pm$

19.7 mm long, 5.8 ± 1.4 mm wide, 1.5 ± 0.8 g damp-dried weight, 6.3 ± 3.1 number of branches, 3.5 ± 2.1 fertile tips per frond, and an overall mean ratio of marginal to surficial pits of 1:19.

Figure 8 compares the primary morphological features of six BBH fucoid taxa and complexes, including the muscoides-like *Fucus* (FMUSC), fragmented *F. spiralis* ecad *lutarius* grading into the muscoides-like plants (i.e., FSL–FMUSC), *F. spiralis* ecad *lutarius*, *F. spiralis*, *F. vesiculosus* ecad *volubilis*, and *Ascophyllum nodosum* ecad *scorpioides*. Frond length, width, weight, and burial depth were smallest in the muscoides-like *Fucus* (Figure 8A–D), averaging 13.2 ± 4.2 mm, 1.1 ± 0.2 mm, 0.11 ± 0.03 g, and 5.6 ± 1.8 mm, respectively. The other five plants showed variable patterns, with frond lengths ranging from 29.9 ± 33.4 mm (*A. nodosum* ecad *scorpioides*) to 78.8 ± 46.4 mm (*F. spiralis* ecad *lutarius*), widths from 1.6 ± 0.8 mm (*A. nodosum* ecad *scorpioides*) to 6.5 ± 5.2 mm (*F. spiralis*), weights from 0.8 ± 1.0 g (FSL–FMUSC) to 4.5 ± 11.2 g (*A. nodosum* ecad *scorpioides*), and burial depths from 9.6 ± 9.4 mm (FSL–FMUSC) to 12.2 ± 19.0 mm (*A. nodosum* ecad *scorpioides*). The number of branches per frond for the five fucoids (Figure 8E) ranged from 6.2 ± 7.5 (*F. spiralis*) to 54.7 ± 84.0 (*F. spiralis* ecad *lutarius*), with the muscoides-like *Fucus* being 4.6 ± 1.1 . Hair pits (Figure 8F) were absent in *A. nodosum* ecad *scorpioides*; the muscoides-like *Fucus* primarily had marginal pits (8.10:0.74 or 11:1, marginal to surficial), while the other four had a prevalence of surficial pits: FSL–FMUSC (16.3:22.2 or 1:1.4), *F. spiralis* ecad *lutarius* (34.3:79.4 or 1:2.3), *F. spiralis* (1.3:24.8 or 1:19), and *F. vesiculosus* ecad *volubilis* (4.7:7.0 or 1:1.5). Reproductive tips (i.e., receptacles) only occurred on *F. spiralis* (0.4 ± 6.4), with these showing a wide range of values (Figure 8G). In summary, the muscoides-like *Fucus* stature (i.e., length, width, and weight) was consistently smaller than the other five fucoid taxa and complexes, while it also had a greater dominance of marginal than surficial pits.

A wide range in morphology is evident in the silhouettes of the three fucoid populations shown in Figure 2. *Fucus spiralis* ranges from young flattened germlings (Figure 2A), to reproductively mature and flattened fronds (Figure 2B), to terete residual and proliferous specimens (Figure 2C). Detached specimens of *F. spiralis* ecad *lutarius* grade from large, fragmented fronds



(Figure 2D), to proliferous and small plants (Figure 2E). The turf-like specimens of the muscoides-like *Fucus* vary from tufted, elongated specimens (Figure 2F), to short, individual fronds (Figure 2G), to minute plants (Figure 2H). Overall, a morphological continuum is evident between attached/proliferous *F. spiralis*, detached/entangled *F. spiralis* ecad *lutarius*, and the muscoides-like *Fucus* (Figure 2A–H); the transition is associated with a diminution of stature, enhanced proliferation, degeneration of residual fronds, and extensive dichotomic splitting (*sensu* Hartog 1972) as noted below.

Analogous morphological variability occurs in *Ascophyllum nodosum* ecad *scorpioides*, with initial detached and slightly proliferous fragments (Figure 3A) becoming highly proliferous (Figure 3B) and these in turn becoming progressively smaller and more residual (Figure 3C, D). The smallest material of *A. nodosum* ecad *scorpioides* is reminiscent of muscoides-like *Fucus* (cf. Figures 2G, 2H, 3D), except that it lacks hair pits (Figure 8F) and is more irregularly branched. Morphological variability in *F. vesiculosus* also ranges from attached and detached fronds (Figure 3E, F), to spiraled fragments of *F. vesiculosus* ecad *volubilis* (Figure 3G), to smaller, residual, and proliferous specimens (Figure 3H). Thus, the pattern of fragmentation, enhanced proliferation, and degeneration of residual fronds within *A. nodosum* ecad *scorpioides* and *F. vesiculosus* ecad *volubilis* is analogous to that previously described (Figure 2). Even so, the smallest fronds of *F. vesiculosus* ecad *volubilis* in BBH (Figure 3H) were always larger than those of the muscoides-like *Fucus* and *A. nodosum* ecad *scorpioides* (Figure 2G, H, 3D).

Transplant studies. Reciprocal transplants of fucoids between +2.0 and +3.4 m above MLW at the 0.40 km BBH site resulted in pronounced morphological changes (Figure 9). Four

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Figure 8. Six morphological features (± 1 SD) of muscoides-like *Fucus* (FMUSC), *F. spiralis* ecad *lutarius* grading into muscoides-like plants (FSL–FMUSC), *F. spiralis* ecad *lutarius* (FSL), *F. spiralis* (FS), *F. vesiculosus* ecad *volubilis* (FVV), and *Ascophyllum nodosum* ecad *scorpioides* (ANS), with the data being expressed as mean frond length (A), width (B), weight (C), burial depth (D), number of branches per frond (E), number of marginal and surficial pits (F), and number of reproductive tips per frond (G).

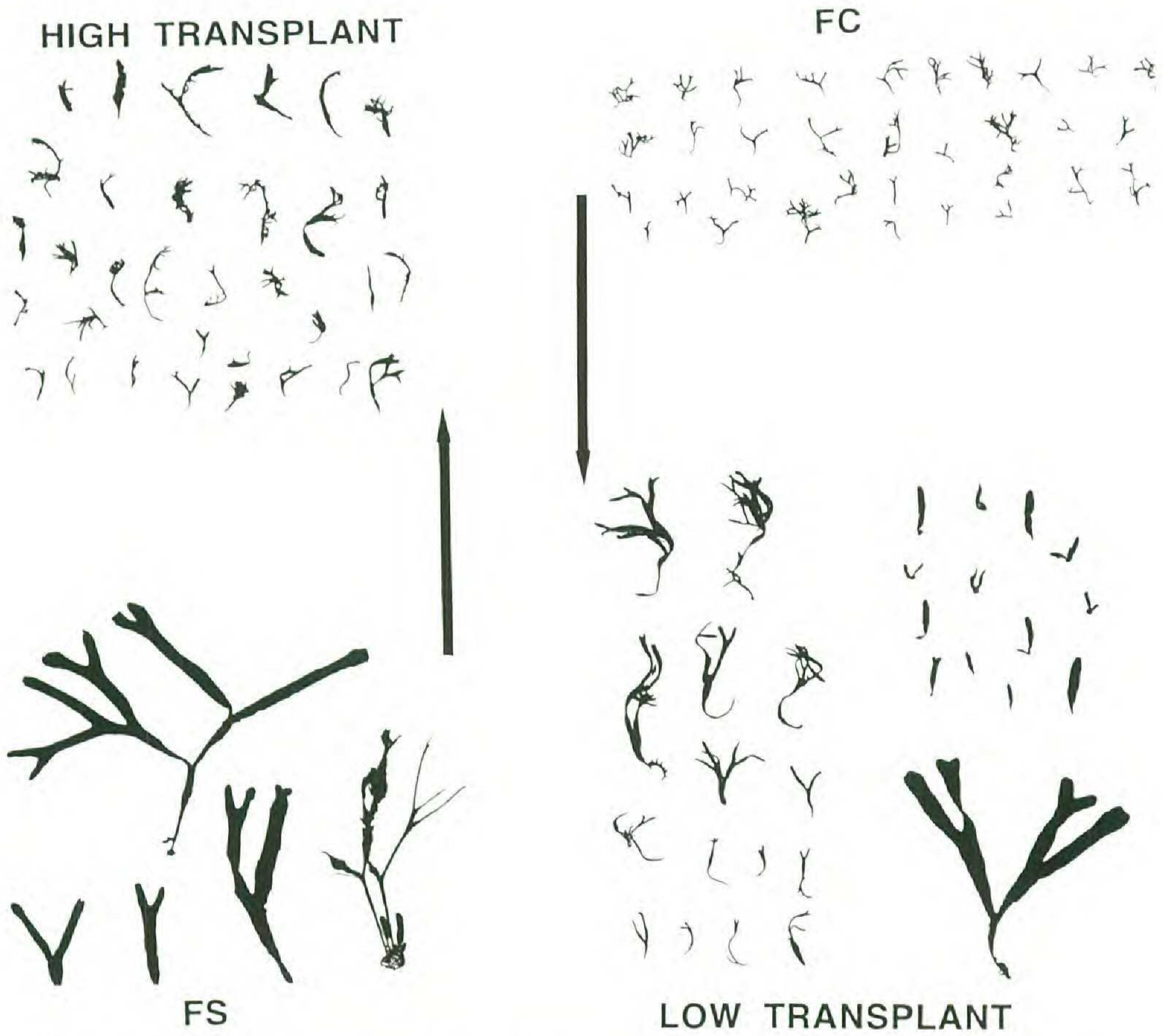


Figure 9. Silhouettes of fucoid plants associated with a reciprocal transplant experiment at a site 0.38 km inland within Brave Boat Harbor's main tidal channel. The results of a transfer of *in situ* *Fucus spiralis* (FS) from the low to high intertidal zone (HIGH TRANSPLANT) are shown in the bottom and top left sides respectively (up arrow). The results of the opposite transfer of *in situ* muscoides-like plants (FMUSC) to the low intertidal (LOW TRANSPLANT) are shown in the upper and lower right sides, respectively (down arrow).

populations were assessed: low *in situ* *Fucus spiralis*, high *in situ* muscoides-like *Fucus*, low transplants of muscoides-like *Fucus*, and high transplants of *F. spiralis*. Low *in situ* *F. spiralis* are longer, wider, and have a greater number of branches and reproductive tips than high *in situ* muscoides-like plants (Figure 10A–C). An analogous pattern was evident when comparing the former plants and the resulting high transplant mixture of *F. spiralis* ecad *lutarius* and muscoides-like plants (i.e., FSL–FMUSC), which was very fragmented, proliferous, and totally vegetative (Figures 2D–E and 9).

In comparing high *in situ* muscoides-like plants with the re-

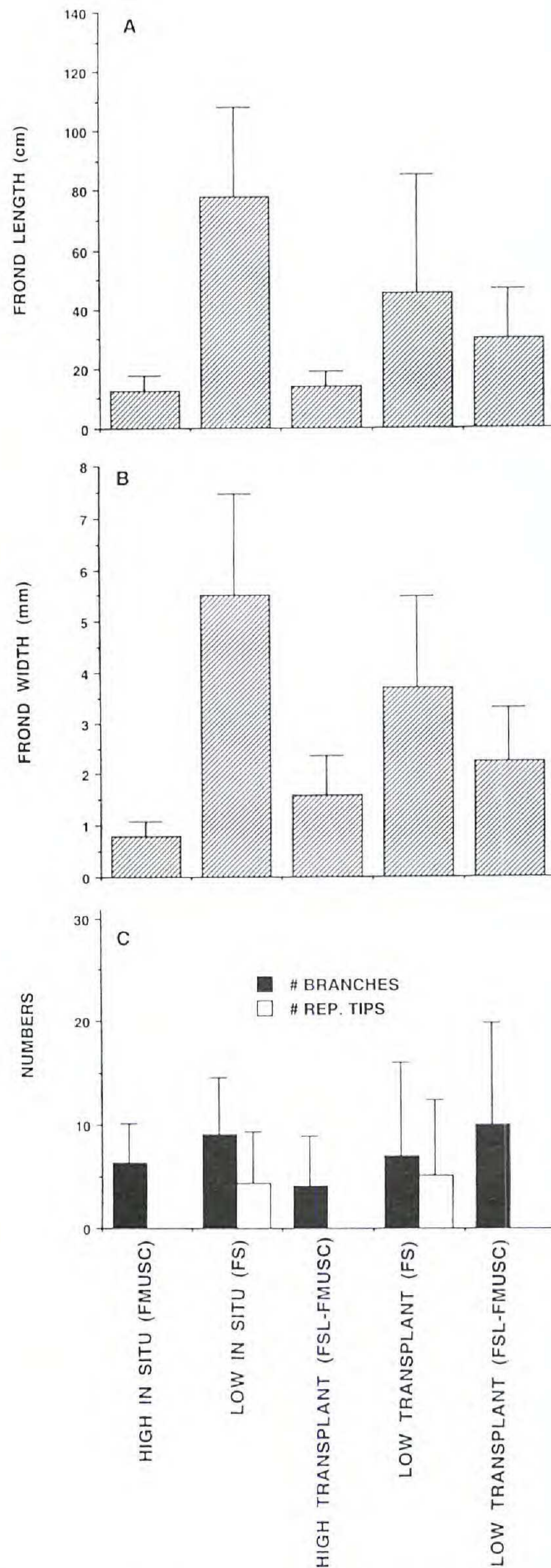


Figure 10. Morphological comparisons (± 1 SD) of five fucoid populations associated with a reciprocal transplant experiment at a site 0.38 km inland within Brave Boat Harbor's main tidal channel. Measurements include mean frond length (A) and width (B), plus the numbers of branches and reproductive tips (C). The plants include *in situ* muscoides-like *Fucus*

sulting low transplants (Figures 9 and 10), four major patterns were evident: (1) low transplants were heterogenous, consisting of newly colonized and reproductive *Fucus spiralis*, plus prolific and fragmented FSL–FMUSC; (2) frond lengths and widths of all transplants were conspicuously greater; (3) the numbers of branches within high *in situ* muscoides-like plants were somewhat reduced versus low transplants of FSL–FMUSC; and (4) reproductive structures were found only on low transplants of *F. spiralis*. The main morphological responses of high transplants were enhanced fragmentation, stunting, proliferation, and reduced reproduction. By contrast, low transplants produced heterogenous material (i.e., FSL–FMUSC and newly colonized *F. spiralis*), and had enhanced frond length and circumscribed reproduction (i.e., only *F. spiralis* was fertile).

DISCUSSION

Our results indicate that the dwarf muscoides-like *Fucus* plants from BBH are phenotypic variants (i.e., ecads) of *F. spiralis*; thus they have a different origin than similar growth forms in Europe originally designated as *F. vesiculosus* var. (ecad) *muscoides* (cf. Baker and Bohling 1916; Cotton 1912; Niell et al., 1980) and now regarded as *F. cottonii* (Wynne and Magne 1991). The dwarf muscoides-like *Fucus* plants have only recently been reported from the Northwest Atlantic (Sears 1998; South and Tittley 1986), with these records being based upon upper salt marsh collections from BBH that were found growing amongst *Spartina patens* (Mathieson et al. 2001). Cotton (1912), who designated a similar plant as *F. vesiculosus* var. *muscoides*, described it as a “remarkable dwarf *Fucus*” that grew on peaty salt marshes above the mean high-tide level at Clare Island, Ireland. He further noted that it was most common in the “best-drained areas” where it formed a “dense mossy turf” amongst several halophytes, being 5–6 cm long, 1–3 mm wide, and “very erect.” While working

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(FMUSC), *in situ* *F. spiralis* (FS), plus resulting plants of *F. spiralis* ecad *lutarius*–muscoides-like *Fucus* (HIGH TRANSPLANT FSL–FMUSC), *F. spiralis* (LOW TRANSPLANT FS), and *F. spiralis* ecad *lutarius*–muscoides-like *Fucus* (LOW TRANSPLANT FSL–FMUSC).

in several marshes in Scotland, Baker and Bohling (1916) recorded a similar dwarf plant, designating it *F. vesiculosus* ead *muscoides*; they noted that it grew “on firm peaty salt marshes as a dense mossy turf.” Lynn (1935) also described a “thick mossy growth” of dwarf plants from Strangford Lough, Ireland, while Wynne and Magne (1991) cited similar features in recognizing this as a distinct species, *F. cottonii*.

In comparing the BBH muscoides-like *Fucus* plants with those from Europe (England, Wales, Scotland, Ireland, and Spain), the New England plants are much smaller (mean = 1.3 ± 0.4 cm long), they primarily occur in the high salt marsh amongst sparse *Spartina patens*, and are only occasionally associated with *Limonium nashii* and *S. alterniflora*. In BBH the plants appear as brown to black branching masses that are embedded (mean depth = 0.6 ± 0.2 cm) within coarse, sandy sediments. Their biomass and horizontal and vertical ranges become more circumscribed with increasing distance inland (Table 3). Regardless of elevation, the muscoides-like *Fucus* primarily grows as an understory plant, mostly within the high marsh. Further inland within BBH estuary (e.g., beyond 0.79 km) the plant is primarily restricted to a narrow band and may be associated with *S. alterniflora*. Typically, the muscoides-like *Fucus* is found on the edges of exposed high marshes in sandy well-drained sediments that exhibit extensive erosion. Using these ecological features we have subsequently located the plant at more than twenty New England salt marshes, ranging from northern Maine to Massachusetts (Mathieson and Dawes, unpubl. data).

Although the dwarf, moss-like fucoid populations recorded for Europe (Baker and Bohling 1916; Cotton, 1912; Lynn 1935; Niell et al. 1980; Wynne and Magne 1991) are probably derived from different species than those found in BBH (Mathieson et al. 2001), they have similar niche characteristics: (1) upper marshes (e.g., the *Spartina patens* zone) that are flooded only by spring tides; (2) regions with reduced water motion; and (3) a substratum that consists of firm, well-drained sediments. Baker and Bohling (1916) speculated that their dwarf habit was associated with low nutrient availability and acidic sediments. However, the well-drained sandy sediments in BBH (see above) suggest that acidity is an unlikely factor, while desiccation and reduced nutrients may be more critical. Our muscoides-like *Fucus* doesn't occur beneath *S. patens* when standing water is evident at low tide, with this

habitat typifying inner, poorly drained marsh. Further, it is uncommon where abundant growths of filamentous algae (e.g., *Rhizoclonium riparium* and *Vaucheria* spp.) grow beneath *S. patens*.

Based upon a variety of morphological observations and the results of our transplant studies we believe that the muscoides-like populations from BBH originate from *Fucus spiralis* via its detached/entangled ecad *lutarius* (Figures 2 and 9). Thus, there is an obvious morphological continuum and spatial proximity between *F. spiralis*, *F. spiralis* ecad *lutarius*, and the muscoides-like *Fucus* (Figure 2A–H), with fragments of *F. spiralis* ecad *lutarius* often occurring embedded near or within dense clumps of dwarf plants. Further, only scattered and inconspicuous populations of *F. vesiculosus* occurred within BBH (see above), while *F. vesiculosus* ecad *volubilis* was only recorded at the 0.86 and 1.12 km transects (Table 1). Transplant specimens exhibited an analogous morphological continuum between the two extreme morphologies (i.e., the muscoides-like *Fucus* and *F. spiralis*) via *F. spiralis* ecad *lutarius* (Figures 2 and 9). Thus, the transplant studies showed the origin of muscoides-like *Fucus* via degeneration and dichotomous splitting (*sensu* Hartog 1972) of *F. spiralis* ecad *lutarius*. The latter process is associated with incremental deposition of sediment, followed by basal frond decay that reaches a dichotomy, effectively separating the frond into two plants (Norton and Mathieson 1983). Our findings differ from Baker and Bohling (1916) and Niell et al. (1980) who proposed a connection between muscoides-like material and *F. vesiculosus*, with the latter paper documenting a morphological continuum between the two plants, the absence of *F. spiralis*, and the presence of only *F. vesiculosus* populations—the opposite of our findings in BBH!

In summary, we believe that the muscoides-like *Fucus* plants from BBH are part of a megaecad (*sensu* Clements 1905) associated with *F. spiralis*. The dwarf form develops within a unique and restrictive habitat, depending upon the availability and type of attached (parental) material. Thus, it appears that a muscoides-like morphology in both Europe and New England can be derived from more than one species (see above). The development of muscoides-like plants from BBH specimens of *F. spiralis* supports Naylor's (1936) observations that the latter species may produce small embedded marsh forms. Analogous patterns of fragmentation, proliferation, degeneration, and dwarfing have also been reported for *Ascophyllum nodosum* ecad *scorpioides* (Lynn

1935), plus the variety *coralloides* Baker and the ecads *libera* Baker (Baker and Bohling 1916) and *muscoides* Skrine of *Pelvetia canaliculata* (L.) Decaisne *et* Thuret (Baker 1912; Carter 1933; Skrine 1929). In describing such fucoids, Naylor (1936) points out that prevailing environmental conditions in salt marshes have tended to produce identical thalli in different species, which are almost indistinguishable in their vegetative state. For example, Carter's (1933) illustration of *P. canaliculata* ecad *muscoides* (Figure 26-1) and those of Wynne and Magne (1991) for *Fucus cottonii* (cf. Figure 1) are very reminiscent of the muscoides-like *Fucus* we have observed from BBH (cf. Figure 2G–H). Further, the small residual materials of *A. nodosum* ecad *scorpioides* from BBH are often difficult to distinguish from muscoides-like plants, except for the absence of hair pits and the more irregular branching (Figures 2G–H, 3D and 8F).

In discussing fucoid taxonomy, Fritsch (1945) has stated that there is considerable confusion regarding the taxonomy of detached/entangled plants like “*Fucus lutarius* Kützing,” with some designating them as *F. vesiculosus* var. *lutarius* (cf. Baker and Bohling 1916; Niell et al. 1980) and others as *F. spiralis* var. *lutarius* (Kützing) Sauvageau (cf. Sauvageau 1907; Taylor 1957). The basis of these different interpretations is their reproductive status, with unisexual plants either being designated as “typical” *F. vesiculosus* or as degenerate hermaphroditic *F. spiralis* (Sauvageau 1907). Aside from this basic reproductive interpretation of species differences, there is also support for a morphological continuum within Cotton's (1912) type material of *F. vesiculosus* var. *muscoides* from Clare Island, Ireland, as pronounced morphological variability is apparent (cf. Figure 2 in Wynne and Magne 1991). Morphological, ecological, and molecular evaluations would help to link the different muscoides-like fucoid algae to their parental plants, which could either be homogenous or heterogenous, depending upon the sites and species present.

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LITERATURE CITED

- BAKER, S. M. 1912. On the brown seaweeds of the salt marsh. *J. Linn. Soc., Bot.* 40: 275–291.
- AND M. H. BOHLING. 1916. On the brown seaweeds of the salt marsh. Part II. Their systematic relationships, morphology, and ecology. *J. Linn. Soc., Bot.* 43: 325–380.
- BONEY, A. D. 1966. *A Biology of the Marine Algae*. Hutchinson Educational Ltd., London, England.
- BORY DE SAINT-VINCENT, J. G. B. M. 1828. Cryptogamie, pp. 97–200. *In*: L. I. Duperry, *Voyage autour du Monde sur "La Coquille"*, Pendant les Années 1822, 1823, 1824 et 1825. Histoire Naturelle, Botanique, Paris, France.
- BRINKHUIS, B. H. 1976. The ecology of temperate saltmarsh fucoids I. Occurrence and distribution of *Ascophyllum nodosum* ecads. *Mar. Biol.* 34: 325–338.
- AND R. F. JONES. 1976. The ecology of temperate saltmarsh fucoids. II. *In situ* growth of transplanted *Ascophyllum nodosum* ecads. *Mar. Biol.* 34: 339–348.
- , N. R. TEMPEL, AND R. F. JONES. 1976. Photosynthesis and respiration of exposed saltmarsh fucoids. *Mar. Biol.* 34: 349–359.
- CARTER, N. 1933. A comparative study of the algal flora of two salt marshes. Part II. *J. Ecol.* 21: 128–208.
- CHAPMAN, A. S. AND A. R. O. CHAPMAN. 1999. Effects of cordgrass on saltmarsh fucoids: Reduced desiccation and light availability, but no changes in biomass. *J. Exp. Mar. Biol. Ecol.* 238: 69–91.
- CHAPMAN, V. J. 1964. *The Algae*. MacMillan and Co. Ltd., London, England.
- CHOCK, J. S. AND A. C. MATHIESON. 1976. Ecological studies of the saltmarsh ecad *scorpioides* (Hornemann) Hauck of *Ascophyllum nodosum* (L.) Le Jolis. *J. Exp. Mar. Biol. Ecol.* 23: 171–190.
- CLEMENTS, F. E. 1905. *Research Methods in Ecology*. Lincoln Univ. Publ. Co., Lincoln, NE.
- COTTON, A. D. 1912. Marine algae, pp. 1–178, 11 Plates. *In*: *A Biological Survey of Clare Island in the County of Mayo, Ireland and the Adjoining District, Section 1, Part 15*. Hodges, Figgis and Co. Ltd., Dublin, Ireland.
- DAWES, C. J. 1998. *Marine Botany*. 2nd ed. John Wiley and Sons Inc., New York.
- FELDMANN, J. AND F. MAGNE. 1964. Addition 'à l'inventaire de la flore marine de Roscoff: Algues, champignons, lichens. Edition de la Station Biologique de Roscoff.
- FRITSCH, F. E. 1945. *The Structure and Reproduction of the Algae*, Vol. II. Cambridge Univ. Press, Cambridge, England.
- GERARD, V. A. 1999. Positive interactions between cordgrass, *Spartina alter-*

- niflora* and the brown alga, *Ascophyllum nodosum* ecad *scorpioides* in a mid-Atlantic coast salt marsh. *J. Exp. Mar. Biol. Ecol.* 239: 157–164.
- HARTOG, C. DEN. 1972. Substratum: Plants: Multicellular Plants, pp. 1277–1289. *In*: O. Kinne, ed., *Marine Ecology*, Vol. 1. Environmental Factors. Part 3. Wiley-Interscience, London, England.
- JORDE, I. 1966. Algal associations of a coastal area south of Bergen, Norway. *Sarsia* 23: 1–52.
- LYNN, M. J. 1935. Rare algae from Strangford Lough. Part I. *Irish Naturalists' J.* 5: 201–208.
- MATHIESON, A. C., C. J. DAWES, M. ANDERSON, AND E. J. HEHRE. 2001. Seaweeds of the Brave Boat Harbor salt marsh and adjacent open coast of southern Maine. *Rhodora* 103: 1–46.
- , ———, AND E. J. HEHRE. 1998. Floristic and zonal studies of seaweeds from Mount Desert Island, Maine: An historical comparison. *Rhodora* 100: 333–379.
- NAYLOR, G. L. 1936. The fucoids of St. John's Lake, Plymouth, including a hitherto undescribed form of *Fucus spiralis*. *Rev. Algol.* 7: 425–439.
- NEWTON, L. 1931. *A Handbook of the British Seaweeds*. British Museum (Natural History), London, England.
- NIELL, F. X., A. MIRANDA, AND J. P. PAZO. 1980. Studies on the morphology of the megaecad *limicola* of *Fucus vesiculosus* L. with taxonomical comments. *Bot. Mar.* 23: 303–307.
- NORTON, T. A. AND A. C. MATHIESON. 1983. The biology of unattached seaweeds, pp. 333–386. *In*: F. E. Round and D. J. Chapman, eds., *Progress in Phycological Research*, Vol. 2. Elsevier Scientific Publ. Co., Amsterdam, Netherlands.
- PARKE, M. AND P. S. DIXON. 1976. Check-list of British marine algae. 3rd revision. *J. Mar. Biol. Assoc. U.K.* 56: 527–594.
- SAUVAGEAU, C. 1907. Sur deux *Fucus* vivant sur le sable. *C.R. Soc. Biol. Paris* 63: 699–701.
- SEARS, J. R., ed. 1998. *NEAS Keys to Benthic Marine Algae of the Northeastern Coast of North America from Long Island Sound to the Strait of Belle Isle*. Contrib. 1, Northeast Algal Society, Univ. Massachusetts Dartmouth Campus Bookstore, Dartmouth, MA.
- SKRINE, P. M. 1929. A member of the Fucaceae from the Dovey salt marshes. *J. Bot.* 67: 241–243.
- SOUTH, G. R. AND I. TITTLE. 1986. *A Checklist and Distributional Index of the Benthic Marine Algae of the North Atlantic Ocean*. Spec. Publ. Huntsman Mar. Lab. and British Museum (Natural History), St. Andrews, NB, Canada and London, England.
- TAYLOR, W. R. 1957. *Marine Algae of the Northeastern Coast of North America*. Univ. Michigan Press, Ann Arbor, MI.
- VALERA, M. DE AND P. J. COOKE. 1979. Seaweed in Burren Gryker. *Irish Naturalist's J.* 19: 436.
- WYNNE, M. J. AND F. MAGNE. 1991. Concerning the name *Fucus muscooides* (Cotton) J. Feldmann *et* Magne. *Cryptog. Algol.* 12: 55–65.